

MACROMIA SPLENDENS (PICTET, 1843) IN EUROPE
WITH NOTES ON ITS HABITS, LARVA, AND
DISTRIBUTION (ODONATA)

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Abstract

A survey is given of the morphology and biology of a large stream-inhabiting Corduliid, the only known representative of its genus in Europe. The history is briefly outlined and the distributional data reviewed. An itinerary relates to two excursions in southern France made in June, 1961 and 1964. New localities are described and field observations are supplied on the flight habits and behaviour. Oviposition was observed twice, but the early larval stages have remained unknown. The taxonomic part contains colour notes as well as illustrations of the hitherto undescribed genital organs and leg structure of the male. An account is given of the larval structures and accompanied by a photograph of the exuvia. The known facts concerning habitat requirements, adaptive features, larval development and life-history of *Macromia* in general are summarized and the relationship of *M. splendens* with other members discussed. The geographical distribution of the insect in south-western Europe is compared with that of its nearest allies of eastern Asia and North America. Most of the localities in France and Portugal are verified and a distribution map is included. The occurrence of the insect in Spain, though not called in question, remains to be re-established.

Since the physiographical and physiological requirements of the larva are closely correlated with a life in slow-flowing streams, it is suggested that *M. splendens* can survive only in low country, with mild climatic conditions prevailing during most of the year. This may explain its restricted and scattered occurrence in the warm river systems of south-western Europe, where it is supposed to have maintained itself as a remnant of a once much richer preglacial fauna. The main factors which are considered derogatory to the insect's survival are explained in connection with the possibility of extinction through over-collecting, a danger easily to be avoided by thoughtful naturalists.

INTRODUCTION

This paper is an attempt to bring up to date our knowledge of *Macromia splendens* (Pictet), a conspicuous dragonfly of great size and beauty, which in 1871 was named 'la Macromie éclatante' by the Baron E. DE SELYS LONGCHAMPS. It is the only European component of a large genus of Corduliidae, a unit of almost world-wide distribution, which takes rather an isolated position both in regard to its morphology and occurrence.

Perhaps the main stimulus to the present account has been furnished by the late K. J. MORTON, who almost forty years ago wrote a concise and interesting article on this insect, a paper also containing a pleasantly composed narrative of his own experiences with it in the field. It will be unnecessary to enter upon the historical part of the subject as this has been fully dealt with in MORTON's introduction from the time of its original description to the date of writing (1925). Subsequent

information has been very scanty with the exception, of course, of the important article published by GRASSÉ (1930), who for the first time gave a description and some illustrations of the larva.

When I had the opportunity, in August 1960, of meeting my friend C. NIELSEN, of Bologna, at the XI. Congress of Entomology in Vienna, we determined to make a joint effort, at some future date, to rediscover *M. splendens* in its natural habitation. During the summer of 1961 I first met with the insect myself in southern France, but it was only after a lapse of two more seasons that both of us succeeded to make a more intimate acquaintance with it. Some of our observations on this subject may be worth putting on record and might be found useful: it is our hope that some of our fellow workers in the south may have the opportunity to fill the remaining gaps in our knowledge of the life history of *M. splendens*. Thus I propose here to give a brief summary of what we learned about it, prefaced by some earlier observations and followed by additional descriptions and notes on the relationship and distribution of this fascinating insect.

STRAY NOTES ON AN EXCURSION IN 1961

While journeying through several of the southern provinces of France in June, 1961 and 1962, I had kept a good look-out for *M. splendens*. The most noticeable event of the first excursion was undoubtedly the rediscovery of our insect near a well-known locality in the département Lot, where MORTON had found it almost forty years previously. On 18th June, 1962, I saw a male at the Vis, near a village called Montmal near Ganges (Gard), but since the insect was not especially worked for, this second trip remained unsuccessful. The next brief itinerary shows the result of the earlier excursion.

About noon of 20th June, 1961, we reached Larroque-des-Arcs, a small village about 5 km east of Cahors at the right bank of the river Lot, where we stayed. The Lot is of course the largest river in the Quercy district and its channel, except when in flood, is usually about 90—100 metres broad. It has turbid water and a slow flow. By the time we arrived no Odonata were seen over the quiet water, but my attention was soon attracted by the noisy behaviour of several Grey Wagtails (*Motacilla cinerea*) tripping about close to the water's edge. A quick search of the small mud flats near the hotel gave the clue to this activity, for glittering patches of wings of freshly emerged dragonflies were scattered over the surface all along the bank. Within a few minutes I picked up a score of *Gomphus* spec. wings, five of *Oxygastra curtisi* and twelve (8 fore and 4 hind wings) of *Macromia splendens*. I have no doubt that these birds here were particularly destructive to the teneral dragonflies emerging and had consumed a high percentage of them. The part of the river on which these adult fragments and larval skins occurred in such profusion is most ordinary in appearance, with no aquatic plants growing in it. Here the Lot flows leisurely through arable land, neglected gardens, etc., and only a narrow fringe of trees and shrubbery grows on its banks.¹⁾ Early next morning the same stretch was again investigated, mainly for exuviae, but apart

¹⁾ A good impression of this site can be obtained from the photographic illustration in the Guide Vert Michelin "Périgord". (1ère édition, p. 120).

from some quite mature *Gomphus simillimus* and a few newly emerged *Gomphus graslini* settled close to the ground or beaten up from among wet grass under the bushes, no imagines of *Macromia* or *Oxygastra* were seen over the water. The *Gomphus* on their maiden flight all headed northwards away from the Lot, crossing the meadows and road, flying in a straight line towards the wooded hills about two hundred yards distant.

We left Larroque early the same morning for Décazeville, following the "route touristique" through the valley of the Lot.

Near Crégols, a charming little village on the left bank about 38 kilometres east of Cahors, a streamlet meandering through woodland branches off from the main river to join it again only half a mile further down. It is a shady stream with clear water flowing over thick deposits of coarse sand, alternating with silt and mud (or even pools in places) and has a luxuriant and varied aquatic vegetation. During summer most of its water is received from a fast flowing brook which comes down from the southern hills, but the debris and dead leaves accumulated between branches of overshadowing trees clearly indicated frequent floods giving rise to rather considerable changes of the water level. It was here, in the afternoon of 19th June, 1961, that I for the first time saw a *Macromia* flying high over the road at some distance from the stream. We returned to the spot on the morning of the 21st and halted for a good search. Only three or four times, with long intervals, a solitary male flew past, and in two and a half hours I had managed to capture only two. They were extremely swift, coursing almost 6 feet high over the middle of the stream. Apart from *Oxygastra curtisi* and the two southern *Platycnemis*, a third species of the latter genus, *P. pennipes*, shared the others. *Calopteryx* was represented by *C. virgo*, and *Cordulegaster boltoni* — which was fairly common — occurred in a small-spotted form very nearly approaching the typical subspecies. Besides *Onychogomphus forcipatus*, also *Gomphus vulgatissimus* (not noted elsewhere) was present. The composite character of the dragonfly fauna met with here strongly suggested a mean temperature of the water much lower than in the open valley of the Lot.

ITINERARY OF A JOINT COLLECTING TRIP IN JUNE, 1964

The aspect that chiefly interested us was the question where to find the breeding sites of *M. splendens*. Also, how to obtain its larva and what would be our chances of capturing a female and keep it alive for eggs. It must be said at the outset that our efforts were only partly rewarded, for although we got a series of males and found some perfect exuviae, a diligent search for a mature female to work out the entire life history remained without success.

Much had to be compressed into a very short space of time (four days in the field), so that we had to make up our minds beforehand as to the most promising spots and the routes to be followed. The valley of the Gardon, with Remoulins and the Pont du Gard area, looked attractive enough as a starting point, the more so since MORTON (1925) reports having twice seen a glimpse of *Macromia* at the Gardon, near the famous aqueduct. We spent part of the sunny, though much too cool, morning of the 25th June at the river but failed to see any. Let alone

other species occurring here, only the presence of many *Sympetrum striolatum* and *Aeshna affinis*, all still more or less immature, seems worth mentioning. Before leaving, two stages of very young gomphid larvae as well as mature ones of *Platycnemis acutipennis* and *Coenagrion* spec. were dredged up from scanty aquatic vegetation and fine sand on the left bank. We then went on via Uzès in a south-westerly direction towards Montpellier, collecting en route. Although the hilly *garrigues* are very arid and barren-looking in most places, we came across two tributary streams of the Gardon, both flowing through marshy land. One of these is the Bourdic, near Aubussargues, the other and more varied one the Crieulon, near Quissac, where we found dragonflies very plentiful and rich in species. The greatest variety we met with at the Crieulon, where we spent the rest of the day and the following morning. Above the dam this stream has wide marshy spots of some extent with a quiet flow, but also shady tracts with clear fast running water over rocky ground. Amongst the many other Odonata occurring here, the most noteworthy — though not the most conspicuous ones — were *Cordulegaster boltoni immaculifrons*, both sexes fairly common, also females ovipositing; *Boyeria irene*, several males not quite matured as well as some exuviae; *Gomphus graslini*, *simillimus*, *pulchellus*, and *vulgatissimus*, the first also taken in cop. and outnumbering the other species. Surprisingly, a pair of what I thought were *G. simillimus*, settling on the path, proved to be male *simillimus* copulating with female *vulgatissimus*. Although we were constantly on the look-out for *Macromia*, I saw it only twice: one male was observed flying swiftly along the path and a second (or same?) specimen, "hanging itself up" behind a pendent tuft of *Galium* under a bridge I missed at close quarters when it alighted.

The late afternoon of 25th June found us at the Source du Lez near Prades (Hérault), the classic locality both of *Macromia splendens* and *Cordulegaster boltoni immaculifrons*.¹⁾ To our regret we found the most promising spots at Prades fenced off and inaccessible, part of the surrounding wood being destroyed by the digging of a reservoir. Though no *Macromia* were seen, *Cordulegaster* was still abundant and we were fortunate enough to make detailed observations on its habits and oviposition, returning to Quissac in the evening.

The next morning, after satisfying ourselves that it was in vain to seek *splendens* any longer at the Crieulon, we decided to proceed to the Quercy area in the northwest part of southern France, a district comprising the river system of the Lot. This location, I reckoned, would probably mean our last chance to meet with *Macromia*. We past most of the day in driving, rain falling nearly all the way. We reached St. Géniez d'Olt, staying the night there, and in the morning of the 27th made for the locality at Crégols whence I had previously obtained a few *splendens* about the same time of the year. Here I found the topography and fauna unchanged, but owing to much rain during the past two or three days the water was high and uncomfortably cold. We spent many hours in the stream bed,

¹⁾ Being in Montpellier in the second week of April, 1961, in company with my friend and colleague Dr. C. O. VAN REGTEREN ALTENA, we visited the ground under the excellent guidance of Dr. A. BOURNIER, of the École Nationale d'Agriculture at Montpellier. On that occasion I for the first time learned the locality and found it was one well worth visiting later in the year.

exploring the surroundings thoroughly in all directions, yet failed to detect any *Macromia*. During the late afternoon and part of the evening we followed the river Lot as far down as Cahors, searching its banks in various places but to our great disappointment found MORTON's location near the town spoiled and the shore vegetation ruined.

In selecting nearby Larroque-des-Arcs as a starting point for further research I had again followed my itinerary of the summer of 1961, a course we had no cause to regret.

On 28th June we were up early and wishing to make the most of our opportunities we decided to have a look at the river first. It was a calm hazy morning and the surface of the water was smooth. The Lot was slightly higher in level than it was in the early summer of 1961, so we found it impossible to walk along its bank. With the exception of a single female of *Gomphus graslini* taken in transformation, we did not see any adult Anisoptera along the river edge, nor were there any predatory birds about. We took a boat and rowing slowly upstream investigated the right bank, looking for exuviae. Covering a stretch of no more than twenty yards in extent our search yielded scores of empty shucks of *Gomphus graslini*¹⁾ and *Oxygastra curtisi*, and if we had wished could easily have collected a hundred or more of the former. The emergence period of these species appeared to have ended already some time before our visit. While not altogether a matter of surprise, I had the good fortune of finding also four exuviae of *M. splendens*, one being attached underneath a landing-stage, a second on the trunk of an alder tree and the remainder adhering with sprawling legs to a weather-stained stone wall below the village. All skins were from 4—7 feet above the water at some distance from the river, and from their withered condition — in one even the head was lacking — it is evident that emergence must have taken place perhaps as much as two weeks earlier.

Not wishing to return to the scene of the previous day's failure, we left the Lot valley after a few hours and, heading towards Figeac, drove into the picturesque valley of the Celé, a strongly meandering tributary which has its source in the granitic hills of Cantal. It enters the Quercy district near Figeac and, breaking through a vast plateau of calcareous rock, continues its tortuous course in a south-westerly direction until running into the Lot above Bouziès. There is a drop in altitude of only thirty metres beginning at a location about fifteen kilometres away from its junction with the Lot, but as is the case with nearly all regional water-courses, there are so many weirs and small dams in its channel that the velocity of flow varies greatly.

The Celé was selected on account of its much smaller size and because of its lower reaches maintaining a moderate flow over a muddy bottom. Since this stream is bordered with trees and protected by high embankments, I also expected its immediate surroundings to be less disturbed by human agency.

¹⁾ Although adult mass emergence of *G. simillimus* in this area takes place somewhat earlier in the season than of *graslini*, *simillimus* too is a common species at the Lot. Yet I am unable to distinguish more than one species in my series of 34 exuviae (20 males, 14 females) collected at random. These agree closely with the skin of the transforming female of *G. graslini*.

We halted at a point near Liauzu, about 8 kilometres upstream, where the valley widened and the distant Celé followed a comparatively straight course. It could be reached from the north through gently sloping meadows at a place where its right bank is flanked by a dense growth of trees and shrubbery. On the opposite side the stream is well protected by hills rising steeply from the south.

We could scarcely have visited this place at a more favourable time. Much rain of the previous days had made the long grass very wet but soon the atmosphere became clear and the rainy weather gave way to ceaseless sunshine during the rest of the day.

Following the narrow tracks down to the steep mud bank, we fortunately found the border open to the sun. To our satisfaction the first *Macromia* was spotted almost immediately. Taking advantage of the tiny promontories used by trout fishermen, it was possible in some places to obtain a fairly secure footing close to the water's edge. We selected different positions at a point opposite a huge wall of solid rock that rose perpendicularly from the water. Here the stream was about 25 metres wide, quietly flowing (approximately 4 km/h near the surface), and carrying fairly deep water that was practically free from vegetation.

M. splendens was evidently at the height of its flying season (i.e., reproductive period) here, and from its habits we got the impression that the locality suited it exactly. Males were readily recognized at some distance, flying steadily up and down the river in regular and long beats. Occasionally one would cross the stream at a certain point in rapid pursuit of prey, but most of them kept to the bank, following the bends and promontories closely one foot or less above the surface. Often they rose, passing gently over more conspicuous obstacles like thickly leaved branches of overhanging trees. Males were over the dark water from the moment of our arrival (about 9.30 a.m.) until we decided to leave (1 p.m.). They became increasingly more numerous as time went on and we were able to collect a fair series. Around 11 a.m. each of us took a male that was followed so soon by a second flying in the same direction that we had no time to secure both. However, short interruptions frequently occurred when two males met and chased each other away, but as far as could be observed both rivals soon returned to the bank and resumed their beat. Clashes with other species occurred throughout the morning, mostly with *Gomphus simillimus* and *pulchellus*, which were seen to be chased away once and again when flying over open water. Frequent clashes also took place with *Oxygastra curtisi*, which was very common; however, males as well as ovipositing females of the latter kept low to the water's surface, usually coming out only in sunlit openings much closer to the bank and then apparently remained unnoticed. Territorial behaviour was not obvious as males continued to fly past fairly regularly in spite of our activities. Once I saw a male *splendens* in pursuit of a mature male of *Gomphus pulchellus*, and at the moment the victim was actually caught from below both were netted in one stroke.

Occasionally there were longer intervals between our captures. These pauses are most likely to be explained by females in the reproductive stage having arrived at the water: individuals of that sex on being seized by chasing males are immediately carried away into the trees. All *Macromia* seen by us had attained sexual maturity, and I estimated that they had been on the wing three weeks.

Oviposition was observed only twice, between 11 and 12 a.m. These were the only instances during which females were at all noticed close by; all the same, they remained beyond our reach on both occasions. The first individual was seen by Dr. NIELSEN who watched it flying upstream in a straight line, about a foot over open water, and forcibly tapping the surface with the end of its abdomen, four or five times at very short intervals. A second female I observed myself ovipositing in a similar way while hovering low down over vegetable debris lodged among dead branches projecting into the stream. It was noticed and disturbed almost instantly in rapid pursuit by a passing male, and I was unable to follow their course.

Exuviae here were not purposely sought for but with more time, perhaps, would not even have been found (see p. 53). However, I collected some empty skins of *Oxygastra* as well as one each of *Boyeria* and *Gomphus graslini*, from tree trunks near the water.

Since our collecting was mainly directed towards obtaining mating pairs or egg-laying females of *M. splendens* in the hope of procuring eggs for breeding purposes, we went on to explore other sections of the Celé during the afternoon. Neither at Marcilhac, however, nor at the bridge a few kilometres after Brengues (both upstream) did we see any more *Macromia*. Reluctantly we were compelled to give up and return home, leaving the sun behind us in the south. Thus, with the suggestion that we should again visit these favoured grounds to learn more in another season, our search for this year had come to an end.

TAXONOMY OF THE ADULT INSECT

Material. — Brussels Museum (Inst. Roy. Sci. Nat., coll. E. DE SELYS LONGCHAMPS): 1 ♀, labelled "Coll. Latreille"; 2 ♂ 2 ♀, "Charente, Delamain"; 2 ♂ 3 ♀ (1 ♀ juv.), "Mp" [Montpellier], 1 ♂ with additional note "fig. Gen. Ins." — British Museum: 1 ♂ 1 ♀, "Charente, Delamain" (ex coll. R. MACLACHLAN). — Leiden Museum: 1 ♂, "Charente, Delamain" (ex coll. DE SELYS); 1 ♂, "Montpellier, Meyer Dür" (ex coll. H. ALBARDA); 1 ♂, Gallia mer., Cahors (Lot), 3.vii.1931, K. J. MORTON (ex coll. M. A. LIEFTINCK); 2 ♂, Gallia mer., Crégols (Lot), 21.vi.1961, M. A. LIEFTINCK (1 ♂ in coll. C. NIELSEN). Leiden Mus. & coll. C. NIELSEN: series ♂, Gallia mer., Liauzu, Celé river (Lot), 29.vi. 1964, M. A. LIEFTINCK & C. NIELSEN; 4 exuviae, Gallia mer., Larroque-des-Arcs (Lot), 28.vi.1964, same collectors. — Coll. Ent., Serv. Florest., Lisbon: 1 ♂, Portugal, Soure, 1—15.vi.1922, A. F. DE SEABRA, labelled "Soure (print) 1-15-6°-922-1185".

In addition to the above, I have had the opportunity, in July 1964, to see the series of *M. splendens* in the MORTON collection that were shown to me by Mr. A. R. WATERSTON, Curator at the Royal Scottish Museum, Edinburgh. Lastly, Dr. K. H. BUCHHOLZ in Bonn wrote me that the species is represented in the collection of the Museum Koenig by a pair from "Charente, Delamain" (ex coll. OBERTHÜR).

Messrs. C. BESUCHET and H. GISIN, whom I had asked to search for the type of *M. splendens* in the collection of the Museum d'Histoire Naturelle at Geneva,

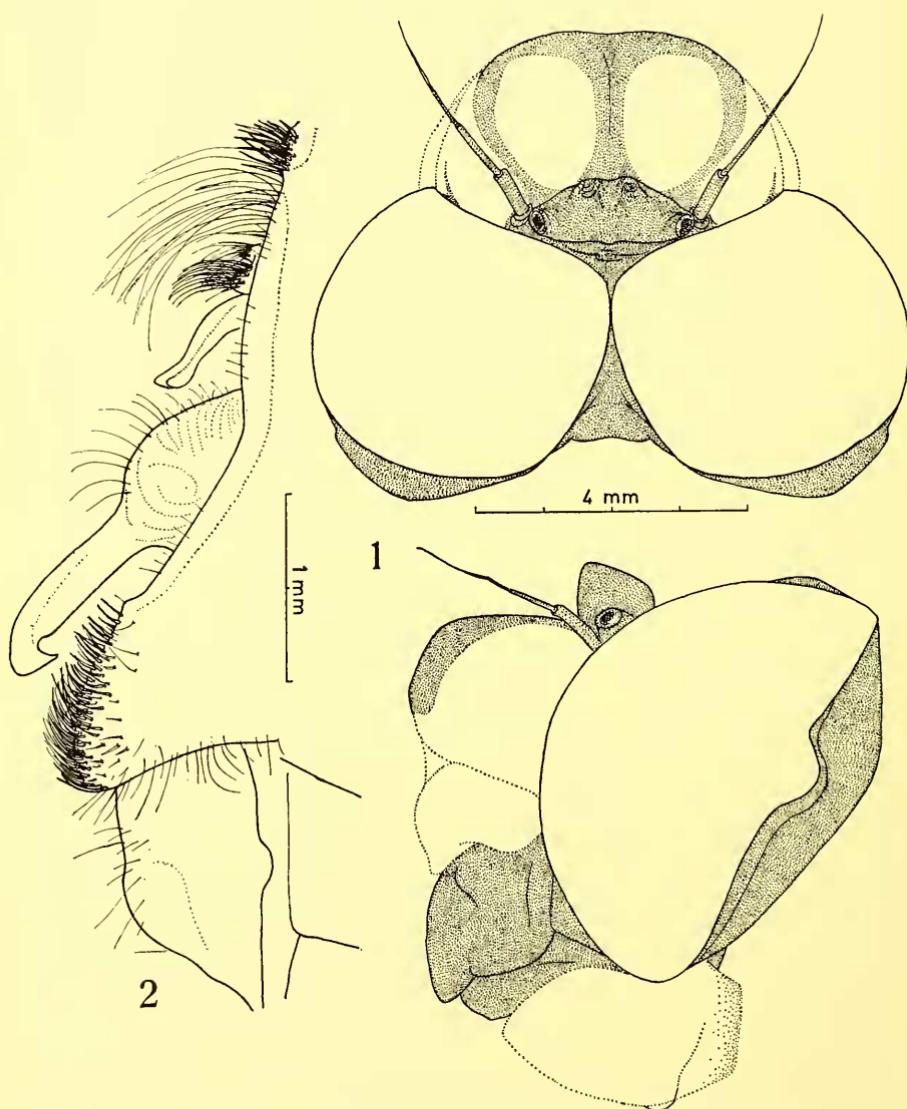


Fig. 1—2. *Macromia splendens* Pictet, ♂ from Crégols (Lot); 1, dorsal and left lateral view of head, showing colour-pattern; 2, left lateral view of genitalia

kindly informed me in a letter that the specimen could not be recovered. Unless the female originating from LATREILLE's collection in the Brussels Museum should prove to be PICTET's specimen, which is not unlikely, the type must be considered lost.

The salient characteristics of colour and pattern are found in the published descriptions (SELYS & HAGEN, 1850; SELYS, 1871). Two coloured illustrations of the whole insect exist in the literature. The first (and best), executed by PRÊTRE, is of the type female and accompanies PICTET's account of the species (1843b). A second, rather crude one, of a male, was given by MARTIN in the Cordulinae volume of the Genera Insectorum (1914). Good drawings of the principal venational characteristics are found in DE SEABRA's paper (1937), which also contains an excellent figure of the anal appendages, all taken from a Portuguese individual. Lastly, a female *M. splendens* caught near Montpellier was recently photographed by RENOUST (1961).

The following morphological details are given in addition to those published earlier.

A feature first attracting attention is the strongly protruding frons, the upper surface of which has well-pronounced lateral ridges. This dorsal part is longitudinally sulcate anteriorly and the two halves on each side of the floor are hollowed out, meeting at an obtuse angle (not shown in the figure 1). The deep black, very feebly metallic, frontal marks are coarsely striato-punctate, while the yellow dorsal patches have an irregularly wrinkled surface.

Male. — Length of posterior femur 12.8—13.2 mm, of anterior tibia 8.2—8.3 mm, of posterior tibia 12.5—13.0 mm; tibia keels yellow, present on distal 40.6% of anterior pair and 80% of posterior pair, but absent on intermediate tibiae. Lateral margin of abdominal tergite 2 with a bunch of strong, closely set, recurved black bristles at extreme base; inner border of genital lobe similarly bristled. Genital organs not prominent, apex of posterior hamule often concealed from view in lateral aspect. Dorsal plate of second penile segment exposed and of large size, shaped like a broad, outwardly convex, almost circularly curled ribbon, the apex of which is widest and truncated; in lateral aspect it is narrow, weakly S-shaped. Basal part of posterior hamule greatly swollen, then suddenly narrowed, cylindrical, at first gently incurved, then again somewhat outcurved, apex slightly twisted ending abruptly in an acute, feebly inwardly directed, recurved tooth (fig. 2).

Wing-membrane hyaline, veins including costa black; membranula white. All triangles and internal triangles uncrossed. Cross-veins in hypertriangles variable, 3—6 (usually 3—4) in fore wing, invariably 2 (not counting internal triangle) in hind wing. Anal loop consisting of 5—9 cells, only occasionally with a central cell. Pterostigma black.

The abdominal segments 4—6 are black; 4 is marked with a pair of small mid-dorsal yellow spots in front of the transverse carina, these spots occasionally being enlarged so as to become confluent posteriorly; 5 usually bears a pair of minute spots placed similarly, but these are wanting in 3 out of 8 freshly captured specimens; segment 6 is unmarked in all individuals examined.

Measurements (14 males, southern France): abd. + app. 52.0—54.5 mm, hind wing 44.5—46.0 mm; pterostigma fore wing 2.3—3.0 mm, pt. hind wing 2.4—3.0 mm.

The Portuguese male from Soure seems to be the only authentic specimen existing in collections of that country. This individual is still in perfect condition, the yellow abdominal markings only being somewhat discoloured. It differs in no way from French specimens. The hypertriangles have a single cross-vein in all wings, the cubital area is traversed by 3 nervures in the fore wings and 2 in the hinder pair; the anal loop contains 6 or 7 cells and the nodal index is 9.14.14.7 in the fore wing, 9.9.8.9 in the hind wing. The yellow spots on the dorsum of abdominal segment 4 are relatively of large size, fused together but narrowly indented by black anteriorly; the spots on 5, though much smaller, are quite distinct and likewise coalescent posteriorly. The succeeding segments are marked similarly to French specimens, 6, 9, and 10 being entirely black, except a pair of small transverse streaks of yellow, one on each side, placed on the ventral surface at extreme base of the 9th tergite. Its measurements are: abd. + app. 50.2 mm, hind wing 45.0 mm, pterostigmata 2.8 mm.

Female. — In all specimens examined the 8th abdominal tergite is without any trace of yellow colouring, thus differing markedly in this respect from the male. The vulvar lamina is very short, with a small U-shaped emargination, the lobes on each side of the latter being represented by a thickening of the posterior edge of the 8th sternite.

The pair in the Museum Koenig at Bonn measure: ♂ abd. + app. 53.5, hind wing 46.0 mm; ♀ 54.0 and 45.0 mm, respectively.

ADDITIONAL NOTES ON THE LARVA OF *M. splendens* Pictet (pl. 4).

The description published by P. GRASSÉ (1930) is very full and accompanied by a good figure of the whole insect and its antenna. GRASSÉ's sketch of the labium being insufficient, I here offer a more detailed one taken from one of the exuviae. These latter correspond closely with the description, except that the number of mental and palpal setae seems to vary. In GRASSÉ's specimen there are 7 + 1—2 mental and 6 palpal setae on each side, while 1—2 additional and somewhat shorter setae are placed at the base of each palpus, followed by 3—6 very minute ones placed in an arc. Our examples agree in all this, except that the number of major setae varies from 7—9 for the mental and 4—5 for the palpal setae. The palpi (lateral lobes) have 6 rounded projections with feebly undulated margins and 5 indentations, the apical projections being again divided while all projections are furnished with 8—11 strong bristles. The frontal horn is conspicuous, erect, the edge between its posterior face and the level surface behind it being approximately a right angle. The eyes are very prominent as are also the tubercles on the postero-lateral angles of the head. The abdomen has strong, almost straight, postero-lateral spines on segment 8 and 9 and dorsal hooks are present on segments 2—10, as shown in the figures.

The colour-pattern in two unsoiled exuviae is as shown in GRASSÉ's picture of a mature larva; it is hardly evident in our photograph as this was taken from a specimen thinly incrusted with fine mud, especially adhering to the legs. The femora bear, however, three indistinct brown bands not shown in GRASSÉ's picture.

Measurements. Total length 31.5 mm, length of abdomen 18.0 mm, greatest

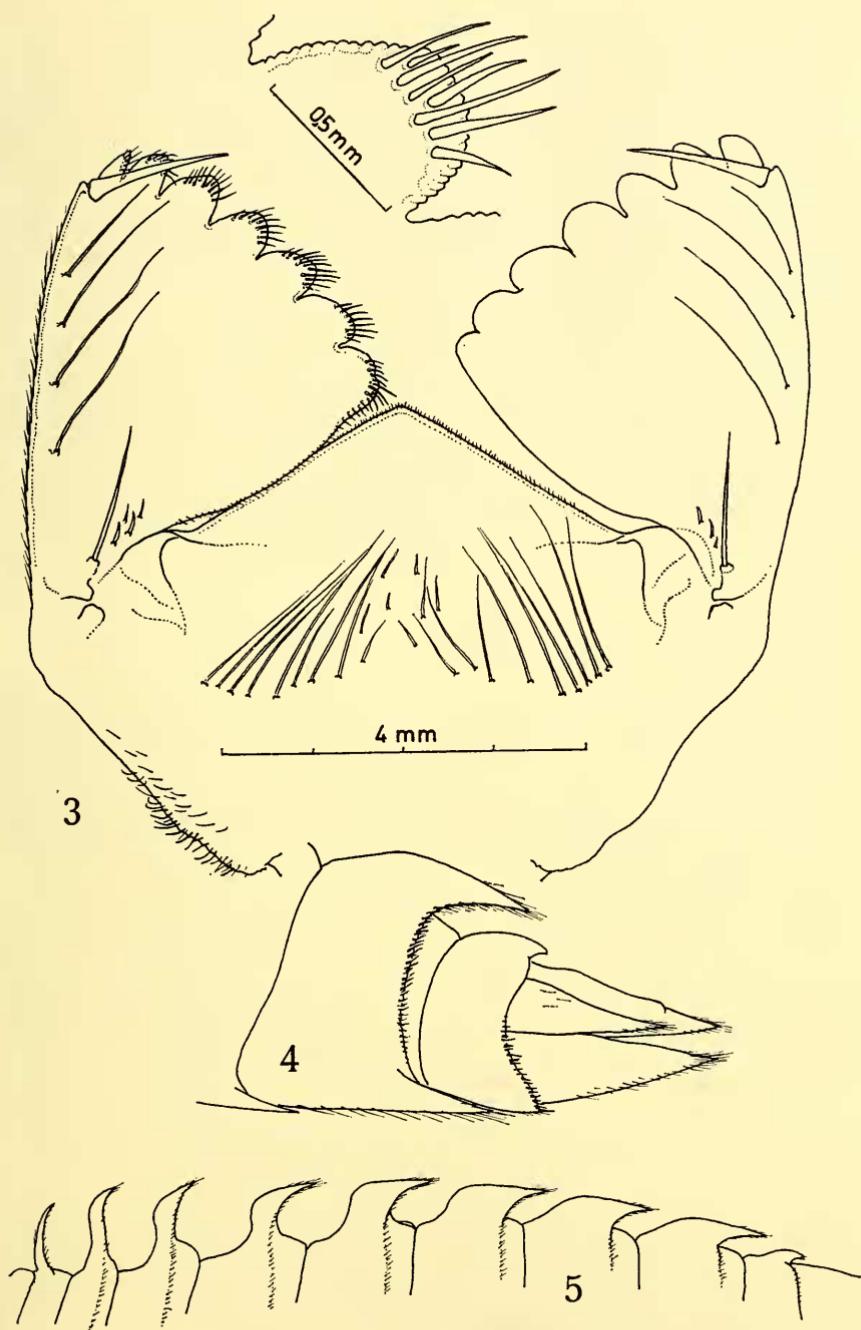


Fig. 3—5. *Macromia splendens* Pictet, ♂ exuvia from Larroque-des-Arcs (Lot); 3, dorsal view of mentum and palpi, flattened out, with 4th setiferous palpal projection more highly magnified (setae on projections of right palpus omitted); 4, left side view of terminal abdominal segments; 5, left side view of dorsal abdominal hooks on segm. 2—10

width of same 12 mm, posterior femur 14.5 mm, and posterior tibia 13.0 mm. (GRASSÉ gives 28,—, 13.5, 14, and 13 mm, respectively, for the larva).

Agrees in general appearance with the supposed larva of *M. manchurica* Asahina (1964), described and figured by POPOVA (1953: 168—171) and with those of the two different species A and B, both from Fukien (E. China) that were discussed and illustrated by myself (1955: 259—263). The differences between these species are best understood by comparing the descriptions and published drawings. The larva of *M. splendens* conforms most closely in the structure of its labium with the Chinese larva B, which also has the meso-metasternal projections reduced to low tubercular swellings. According to ASAHIKA's (1959: 85) figures of the Japanese *M. daimoji* Okum., the dorsal hooks on the abdomen are smaller (and absent on segment 10), while the marginal projections of the labial palpus appear to be more deeply indented. As far as I am aware from the literature, the larva of *M. amphigena* Selys has never been sufficiently characterized (FRASER, 1936). Of the described larvae in the New World species (see WALKER, 1937), *M. splendens* seems to come nearest *illinoiensis* Walsh and *rickeri* Walker, more especially to the former, but the strongly upcurved frontal horn of *splendens* is not acute at its apex, the dorsal abdominal spines are longer and more abruptly curved backwards, and there are also differences in the labial structure.

GENERAL REMARKS

Much, still, has to be learned about the life history of *M. splendens*. Interesting observations on the habitat and ethology of *Macromia* in temperate regions, adults and larvae, are to be found in the publications of KENNEDY (1915), WALKER (1937), WHITEHOUSE (1941) and WILLIAMSON (1909). Only nearctic forms are dealt with by these authors. More detailed information relating to tropical Asiatic species of *Macromia*, particularly on the adaptive features exhibited by their larvae, is supplied by LIEFTINCK (1950).

Very few investigations have yet been made on the habitat of the earliest instar larva of macromiine dragonflies, only that of the allied genus *Epophthalmia* having been described and figured (LIEFTINCK, 1931: 76—79, fig. 25—27). Morphologically this differs considerably from the full-grown stage, showing curious adaptations to its environment. This point in particular is well worth attention when it comes to working out the complete biology of *M. splendens*.

I have failed to find any record in the literature on *Macromia* about the duration of larval life; hence, for the time being any opinion concerning the life cycle of its members must remain a conjecture. To me it seems most probable that the warm temperate forms of *Macromia* conform to a type of life history known to exist in the summer species among the Corduliidae and Gomphidae which occur at more northern temperate latitudes. This would imply that different sizes of overwintering young larvae can be found in any suitable habitat at a time when adult dragonflies of an older generation are on the wing.

As far as tropical species are concerned, we know for certain that in all riverine habitats showing no marked seasonal fluctuations of atmospheric or water temperature, there is a continuous succession of generations throughout the year. But even so, breeding experiments

carried out by me in Java and Malaya with larvae in different stages of development pointed to a relatively long life cycle. Without exception individuals reared in captivity under optimal conditions of food showed the last two or three larval instars to move, feed and grow remarkably slowly. Thus in two young larvae of *M. cincta* Ramb. from South Sumatra, the antepenultimate instar took an average of 90 days. Specimens of *M. moorei fumata* Krüg., dredged up as full-grown larvae, required 65—82 days before transformation took place. Similarly, a male of *M. gerstaekeri* Krüg. in the ultimate instar was bred out only after 85 days. As these mature larvae were collected already some time after the last ecdysis had taken place, the total life-span of the last instar must have been even longer. The most extended period of life ever recorded for a *Macromia* larva in the final stage was that of the lowland species, *M. arachnomima* Lieft., from S. Borneo, which lived 120 days from the date of its capture till transformation, its emergence being preceded by a period of complete dormancy which lasted 30—40 days. (See LIEFTINCK, 1950 : 676, and 1953 : 406.)

Of course, the above facts only serve as guide in future studies of the total duration of larval life in *Macromia*; but we may, perhaps, infer from what we know of reared specimens in the tropics that the palaearctic *M. splendens* normally is either semivoltine or even has a larval period occupying three years. Inclement winters may cause the insect to be met with in numbers only in certain spaced years when a major emergence has taken place.

Regarding our species, I have little hesitation in expressing the opinion that at least its later larval stages develop and reach maturity in the quieter and warmer rivers, whence the perfect dragonflies on emergence scatter themselves over a wide area in search of food and shelter. After this "pre-reproductive period" (CORBET, 1962 : 120), adults return to the breeding sites. Several authors have called attention to the fact that after the maturation period, the imagines of rheophilous insects tend to migrate upstream, working towards swifter waters. This tendency of upstream migration of adults in the reproductive stage has been observed in unrelated groups and may serve to offset the washing down of larvae during times of heavy flooding when aquatic stages may become dislodged and swept away by the current. (See, for instance, KENNEDY, 1917, for Nearctic Gomphidae; INE, 1940, for Nearctic Ephemeroptera; LIEFTINCK, 1941 and 1950, for Malaysian Gomphidae and *Macromia*, respectively.) It is possible that *Macromia splendens* under certain circumstances shows a corresponding behaviour.

In view of the fact that the exuviae found on the present occasion are only thinly coated with mud particles, the older instar larvae most likely are only superficial burrowers or dwell among benthic material on bottoms of a distinctly soft, muddy character.

RELATIONSHIP

Any attempt to ascertain the affinity of *M. splendens* with other species of this widely distributed genus can only be arrived at after a searching investigation into colour, venation and, above all, details of structure. Many species have been described in great detail but we are less informed about the morphology of the head and legs, while the structure of the reproductive organs of both sexes have not for each taxon been studied and figured in sufficient detail. There can be no doubt, however, that *splendens* is most nearly related to its congeners occurring

in the temperate regions. All of these differ markedly in several respects from the tropical groups within the genus.

Considering first the North American members of *Macromia*, the key characters employed by WALKER (1937) and WESTFALL (1947), though quite useful, are mainly based on colour. I have for comparison six out of the ten species known in the adult stage. With the exception of *M. taeniolata* Ramb., these correspond fairly well in general appearance and body structure, the projecting frons with its pronouncedly flattened and rimmed surface being especially noteworthy. Yet each of them shows a combination of characters not shared by *splendens*, suggesting only remote affinity. On examining the wealth of tropical *Macromia* for some indication as to the relationship of these forms, I have often found it difficult to judge which of their specific characters should be considered most important, for one is met by the remarkable fact that these features are variously mixed. As far as structure is concerned, the following example may demonstrate the difficulty in associating our species with any of the New World members. *M. magnifica* Mac Lachlan and *rickeri* Walker differ from the eight others by having no keel on the flexor side of the middle tibia, agreeing in this respect with *splendens*; at the same time these two species show no sign of an external tooth at the superior appendage, whereas in *splendens* (and most of the remaining nearctic species as well) such a tooth is conspicuously present. All I can say at present of these North American members is that *magnifica*, *rickeri* and *wabashensis* show the nearest approach towards the European species.

Turning now to the Old World members of the genus, the reader may be referred to an earlier paper (LIEFTINCK, 1955) in which are listed all species then known to occur in the far north-eastern countries of Asia. On that occasion it was pointed out that *M. amphigena* Selys, *fraenata* Martin, *sibirica* Djakonov, *daimoji* Okumura and possibly a few others of unknown status, belong to a group having mainly a palaearctic distribution. In a recent paper, ASAHIKA (1964) treats the Korean *fraenata* as a subspecies of *amphigena*. He also describes two new species, *kubokaiya* from the Ruykyus (Okinawa) and *manchurica* from East Manchuria, the latter possibly coinciding with a larva from Lake Hanka described and figured — but left without a name — by POPOVA (1953). They form a group of allied species but differ among themselves correspondingly to those occurring in the nearctic region. *M. daimoji* and *manchurica* agree with *splendens* by having a simply hooked posterior hamule and no keel on the mesotibia; both are, however, more slender species with shorter wings. *M. amphigena* and *fraenata* on the other hand, have the facies and robust build of *splendens*, the latter even exhibiting yellow marks on top of frons, but in them the frons is shorter and more rounded, and they also possess a hammer-shaped hamule and mesotibial keel, thus differing markedly from *splendens*. Considering all this, we arrive at the conclusion that *M. splendens*, though having many features in common with the northern nearctic and north-eastern palaearctic members of the genus, stands apart from all others. Of all known species it resembles the Japanese *amphigena* most closely in stature and markings.

DISTRIBUTION

As to the distribution in France, DE SELYS (1871 : 185) already says: "entre le Languedoc et la côte de Bretagne, sur une bande étroite", the closing sentence, perhaps, suggesting a line of thought elaborated much later by MORTON after his discovery of an intermediate location. He wrote as follows: "... It may be expected with some confidence to occur on other tributaries of the Garonne rising in Central France, such as the Dordogne and the Tarn. And there seems to be no good reason why it should not still occur on the Charente. Perhaps there is less probability of its existence in the rivers which have their sources in the higher Pyrenees, as these are probably liable to be cooled by snow water to a later period in the summer than those rising in Central France." (loc. cit.: 15). These comments on the possible extent of its range are interesting and may prove to be quite true as no single record is yet known from the tributary streams arising in the south.

From what has been communicated by MORTON and later observations, it appears that the species in two distant places where it formerly occurred is still thriving. The northernmost records, Jarnac (Charente) and "Anjou" are almost a century old and have never been confirmed, but even at present there seems to be nothing to account for its disappearance there. MORTON relates to a specimen said

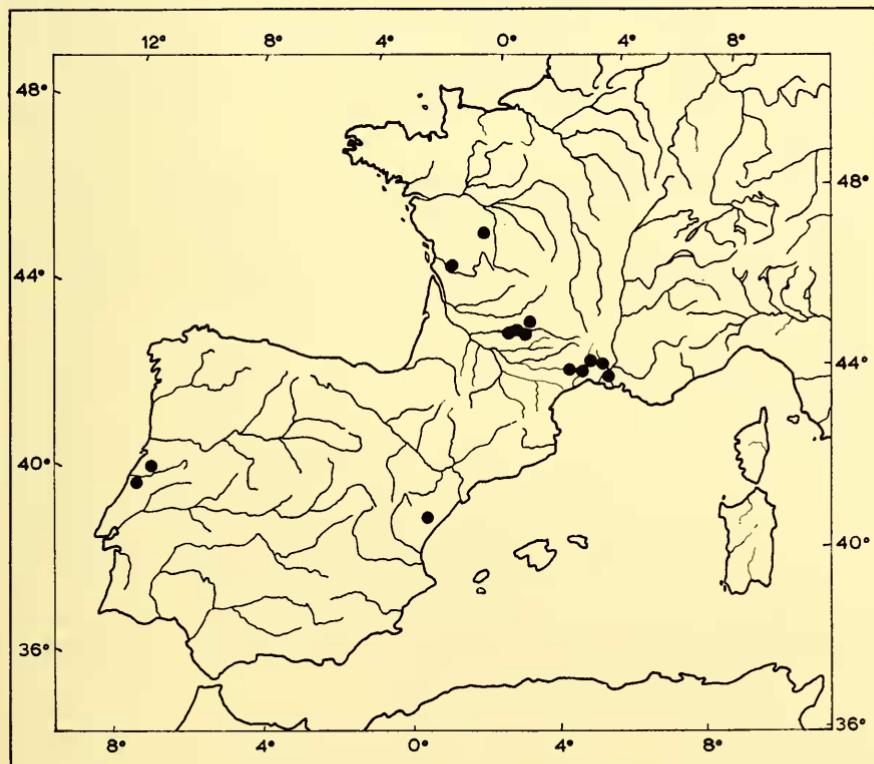


Fig. 6. Map of southwestern Europe showing the known locality records of *Macromia splendens* Pictet

to have come from the "Bouches du Rhône", which he saw in MAC LACHLAN's private collection. This might still be found amongst the accessions, but the only specimens I could find in the British Museum and which are now incorporated in the general collection, are the pair from Charente taken by DELAMAIN (1868). These formed part of a long series, of which several were presented by DE SELYS LONGCHAMPS to his personal friends and correspondents.

The accompanying map (fig. 6) indicates the isolated occurrence of our species in western Europe. It is only a preliminary conspectus and the gaps in it will of course be filled up by future observations, but it gives all localities at present known, including the old Iberian records of NAVÀS (1923, 1924) and DE SEABRA (1937). I have had no opportunity as yet of examining any Spanish individual of *M. splendens*. NAVÀS (1923 : 9) reported it from Segorbe (Castelló), but Dr. PAU, from whom the specimen was received, informed him that it might also have come from the Serra Camarena. In a letter to MORTON the same author wrote that he believes this unique Spanish (Catalonian) example was taken in June or July (MORTON, 1925 : 15). Prof. G. CEBALLOS informed me in a letter that the species is not represented in the Instituto Español de Entomología at Madrid. Sr. A. COMPTE SART even asserts that no specimens could be traced in any of the entomological collections of the museums in Barcelona (Museo de Zoología) or Madrid; he adds that NAVÀS's collections at the Jesuit's Colegio de Salvador (Zaragoza) were partly destroyed and that there was no possibility to verify the rest that was divided up between the Colegio at Zaragoza and the Barcelona Museum. Thus all my inquiries into the whereabouts of an authentic Spanish individual of *M. splendens* remained ineffectual.

As to the Portuguese records of our species, these are apparently based only on two specimens, one discovered by the late Prof. A. F. DE SEABRA near Soure, a coastal locality west of Coimbra, and a second cited by Padre NAVÀS as from "Poigres", which according to Dr. DINIZ (in litt.) undoubtedly should be Poiares (Beira Litoral), about 25 km east of Coimbra. The specimen examined by me is the one from Soure, which was probably taken at the Rio Mondego.

In the northern hemisphere three Nearctic species, namely *illinoiensis* Walsh, *magnifica* Mac Lachlan and *rickeri* Walker, penetrate into the Canadian zone between lat. 49° and 50° N, but even the wide-ranging *illinoiensis* does not extend beyond the Hudson Bay watershed, and no species have so far been recorded from the subarctic region. On the mainland of the eastern Palaearctic, the Japanese *amphigena* Selys occurs as far north as the lower reaches of the Amur (about lat. 50° N). *M. sibirica* Djakonov apparently has a more westward distribution, for it is recorded from a large area between the Baikal Lake and the wooded districts of the Jenisei and Ob, near Novosibirsk (long. 83° E, lat. 55° N), which at the same time is the northernmost locality for any *Macromia* and the point least remote from the habitat of *M. splendens*.

To sum up shortly: *M. splendens* is the only representative of *Macromia* in Europe, its nearest relatives being found in the temperate parts of the Nearctic and eastern Palaearctic. The available evidence indicates that the insect is geographically restricted to those areas of southwestern Europe that have a mild climate (SW. France, W. Portugal and E. Spain). It is apparently confined to the

plains and hills not above 300 metres, frequenting streams with a slow current, in which it also breeds. In view of its scattered distribution the insect could probably only maintain itself in the warmer parts of its range, where the climate is most uniform in character, and it is conceivable that *M. splendens* represents an Eurasian remnant of a much richer preglacial (Late Pleistocene) fauna whose constituents became largely extinct as a result of the colder climate during the last pleistocene glaciation.

One point remains to be considered. I have been advised not to notice the special localities of *M. splendens* in any detail, because, once the attention has been drawn to its haunts, an invasion of *Macromia* hunters would be unavoidable, and this may hasten its decline or even cause its extermination. Collectors in the early days were few, whereas at present every corner of a country has its eager explorer, either resident or visitor.

Of course, species of localized distribution requiring a particular kind of soil or food-plant to live on are, indeed, in real danger even in France. There are notable examples among butterflies and beetles which in localities where they were plentiful in former times are now gradually disappearing. It is true that *M. splendens* exists in a comparatively limited area of France and to a certain extent is of local occurrence even in that country. But, first of all, there is no evidence for considering it to be an insect once more or less widely distributed that has gradually become more narrowly localized. Localization may generally be looked upon as the first step to extinction, but in our case the restricted occurrence is, I believe, due to natural physical conditions, such as topography and climate. No doubt the nature of the stream-bed in combination with a high average yearly temperature of the water and an abundant supply of food are the most important factors contributing to its maintenance. As to the principal cause that may precipitate its destruction and lead to its extinction, I cannot but think that these are brought about directly by man's agency. Industrialization and the pollution of streams as well as the establishment of modern "recreation" centres in suitable localities may ultimately prove fatal. Fortunately, the species mainly abounds in a country where there is neither an extension of towns or industry, nor an excessive cultivation needed for a rapidly increasing population. It may be remembered also that in the Midi of France and towards the south there is a multitude of streams, many of them still unexplored and difficult of access. Needless to say, *M. splendens* is a swift and strong flier which easily escapes notice. In connection with this it would appear to me that overlapping of generations will prevent the species from becoming extinct and that the chances of its utter annihilation through over-collecting are remote. In this particular case all I would implore collectors is to refrain from taking the females, unless there is a positive reason for so doing. Let us hope that disaster, physical or otherwise, may long be absent, and so avert its extinction!

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